# Upward movement of underground plant parts into deposits of tephra from Mount St. Helens

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The burial of plants is seldom studied but is potentially important in some ecosystems. For each of eight herbaceous species, about 10 individuals that survived burial by 7–15 cm of tephra were totally excavated during both 1981 and 1982. The long rhizomes of *Achlys triphylla*, *Clintonia uniflora*, and *Smilacina stellata* grew upward at an angle, so that 7% of rhizome and 3% of root dry weights were in the tephra in 1981; these values increased to 23 and 19%, respectively, in 1982. Burial reduced the number of shoots produced by each plant. Stolons of *Rubus lasiococcus* grew straight up and then spread across the tephra surface, although few roots were produced in the tephra. Plants of *Arnica latifolia* quickly moved rhizomes and roots into the tephra; 50% of underground dry weight was in the tephra by 1982. In two species with short rhizomes (*Tiarella trifoliata* and *Valeriana sitchensis*) there was an altered growth form; the rhizome elongated rapidly straight up to the tephra surface. The corm of *Erythronium montanum* was not relocated upward and it produced no roots in the tephra.

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L'ensevelissement des végétaux est rarement étudié, mais il est potentiellement important dans certains écosystèmes. Pour chacune de huit espèces herbacées, environ 10 individus qui avaient survécu à l'enfouissement sous 7–15 cm de tuf volcanique en ont été extraits au cours des années 1981 et 1982. Les longs rhizomes des *Achlys triphylla*, *Clintonia uniflora* et *Smilacina stellata* avaient poussé vers le haut à un angle, de sorte que 7% du poids sec rhizomateux et 3% du poids sec radiculaire se trouvait dans le tuf en 1981; ces valeurs augmentent à 23 et 19%, respectivement, en 1982. L'ensevelissement avait réduit le nombre de pousses produites par chaque individu. Les stolons du *Rubus lasiococcus* avaient poussé directement vers le haut et puis s'étaient étendus sur la surface du tuf quoique des racines étaient rarement produites dans le tuf. Les plants de l'*Arnica latifolia* produisent rapidement des rhizomes et des racines dans les cendres où l'on retrouvait, rendu en 1982, 50% du poids sec souterrain. Chez deux espèces à rhizomes courts (*Tiarella trifoliata* et *Valeriana sitchensis*), nous avons noté en changement du port: le rhizome s'était allongé rapidement directement vers le haut et jusqu'à la surface des dépots volcaniques. Le bulbe plein du *Erythronium montanum* n'avait pas subi de déplacement vers le haut et il n'y avait pas eu de production de racines dans les cendres.

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## Introduction

Although plants are seldom buried in most habitats, sand dune movement, alluvial deposition, dust storms, and volcanic activity all may bury plants over extensive areas (Antos and Zobel 1985*a*). Often the deposits are shallow enough that plants can survive if they adjust to the altered environment. Survival and function after burial is determined, in part, by growth form. Burial must induce some modification in growth if the perennating buds of herbaceous plants are to regain their normal position relative to the new surface (Antos and Zobel 1985*b*). Survival can occur without adjustment of bud location, but if deposits are deep, recurring annual shoot penetration may not be feasible.

Little information exists regarding morphological changes resulting from burial of plants. Burial is sufficiently chronic in sand dunes that some species have become adapted to the situation. A few species of dune grass lose vigor if not buried annually; they produce new rhizomes and adventitious roots from the buried culms (Martin 1959; Marshall 1965; Hope-Simpson and Jefferies 1966; Godfrey and Godfrey 1976). During the 1930's drought on the American Great Plains, dust deposits only a few centimetres deep destroyed most buried vegetation (Weaver and Albertson 1936); most surviving individuals had moved their perennating buds upward (Robertson 1939; Mueller 1941). Several studies have described changes in the composition of vegetation induced by volcanic burial (Brown *et al.* 1917; Griggs 1918, 1919*a*, 1919*b*; Eggler 1948, 1963; Smathers and Mueller-Dombois 1974); they provided little detail about how plants survive, except to indicate that woody species tend to produce adventitious roots in the deposit and herbaceous species also tend to move root systems upward.

Considering the paucity of detailed information on morphological changes resulting from plant burial, we examined the movement of individual plants into the tephra for eight common forest species of contrasting growth form. Our specific objectives were to determine (*i*) the extent and manner of movement of the different plant parts into the tephra by the second and third season after the eruption, and (*ii*) how a species' reaction to burial is related to its normal growth form.

## Methods

The eight species that we studied represent a variety of growth forms, which are described in detail in Antos and Zobel (1984). *Achlys triphylla* (Berberidaceae; nomenclature follows Hitchcock and Cronquist 1973) and *Clintonia uniflora* (Liliaceae) have long rhizomes from which the deciduous leaves arise; stem tissue emerges above ground only as the flowering stalk. *Smilacina stellata* (Liliaceae) also has long rhizomes but the deciduous leaves occur on determinate aerial stems. *Rubus lasiococcus* (Rosaceae), with stolons that grow on the forest floor, has small, partly evergreen leaves. All species described so far maintain extensive rhizome or stolon systems connecting several aerial shoots. *Arnica latifolia* (Compositae) has long rhizomes but the connected rhizome systems are smaller because of shorter rhizome life-span. Its rhizomes turn upward to form aerial shoots that produce deciduous leaves for a number of years. *Tiarella trifoliata* var. *unifoliata* (Saxifragaceae) and *Valeriana sitchensis* (Valerianaceae) have short rhizomes near or at the soil surface. *Erythronium montanum* (Liliaceae) has a short, segmented corm.

All species except *Smilacina stellata* were examined in old-growth *Abies amabilis* forest at about 1200 m elevation, 22 km northeast of Mount St. Helens. The 18 May 1980 eruption of Mount St. Helens covered the area with 12–18 cm of tephra consisting of (*i*) a silty basal layer approximately 1 cm thick; (*ii*) a 10–16 cm thick layer of sand- to gravel-sized pumice, with fragments exceeding 1 cm in diameter; and (*iii*) a silty crust about 1 cm thick which hardened when dry. The basal layer and crust impeded both drainage and penetration of shoots. Although the forest originally had a luxuriant, diverse herb layer, most herbs did not emerge after burial. The tree canopy was not seriously damaged in the study area. The climate is wet maritime with a pronounced winter precipitation maximum and deep winter snowpacks.

*Smilacina stellata* did not occur at the main study site but is a common species in the region; we examined plants in old-growth forest with 7.5 cm of tephra at 800 m elevation.

Few plants emerged through the tephra, so we excavated any plant we could find provided it (*i*) was in good condition, i.e., leaves were intact; and (*ii*) had grown through tephra of normal depth. Many plants were rejected because the shoots emerged either around buried debris which aided penetration of the tephra or through a deposit thinned by erosion. We totally excavated 5–15 individuals of each species during August and September in both 1981 and 1982. The number of individuals sampled varied because of both plant abundance and the time required for excavation. We excavated members of a species in the same locality in both years and excluded flowering plants, except for *E. montanum*, in order to maximize comparability of the data. We excavated whole plants (all physically connected parts) because it is not possible to divide the underground rhizomes among ramets in the species with complex rhizome systems. Also, we feel that the whole connected system is the most appropriate unit to consider as an individual in the examination of upward movement of plants into the tephra.

Once an aerial shoot has been chosen we carefully excavated all attached parts using a variety of hand tools. We dug as many of the roots as possible; the vast majority of root weight was recovered in all species except *E. montanum*, which had exceedingly thin, brittle roots. *Valeriana sitchensis* also had brittle roots which resulted in larger losses than for other species.

During excavation we recorded characteristics of the rhizomes, stolons, corms, aerial shoots, and tephra associated with each aerial shoot. Particular attention was paid to the locations where plant parts entered the tephra. All stem and root measurements were made during excavation. The plants were separated into leaves, stem (rhizome, stolon, or corm), roots, and other parts where appropriate, and parts were segregated according to their location in the air, tephra, or pre-1980 soil. All plants were washed thoroughly within a few hours and promptly dried at 70°C for about 24 h. They were redried for an additional 24 h or more immediately before weighing.

To determine the normal growth form of the eight species, we examined plants in 1981 and 1982 in the Oregon Cascades, outside the area affected by tephra, in forests with elevation and composition similar to those affected by tephra (Antos and Zobel 1984); these we refer to as control plants. Here, only selected data from control plants are presented for comparison.

The size data for many species were not normally distributed; often there were one or two exceptionally large plants. Consequently, we used the nonparametric Mann–Whitney *U* test (Sokal and Rohlf 1981) for all comparisons that involved weight, size, or number of parts. When analyzing percentage weight data, we used a two-tailed *t*-test for comparisons between groups within species. For comparisons among species, Duncan's multiple range test was used. The arcsine transformation was applied to all percentage data before analysis (Sokal and Rohlf 1981). All analyses were performed using SPSS programs (Nie *et al.* 1975).

## Results

### *Distribution of total plant weight*

*Achlys triphylla* and *Smilacina stellata* had the heaviest rhizome systems; *Erythronium montanum* plants were the smallest (Table 1). *Smilacina stellata* control plants were much heavier than the plants found in tephra, because of two very large individuals (56 and 26 g).

TABLE 1. Mean total dry weight (grams) of plants in tephra and at control sites

| | Tephra, 1981 | Tephra, 1982 | Control |
|---|---|---|---|
| *Achlys triphylla* | 7.6±5.4* | 7.7±5.7 | 7.3±4.5 |
| | (7) | (7) | (9) |
| *Clintonia uniflora* | 1.9±0.7 | 1.5±0.5 | 2.7±2.8 |
| | (5) | (8) | (10) |
| *Smilacina stellata* | 4.3±3.3 | 3.3±3.1 | 18.3±18.0 |
| | (9) | (8) | (7) |
| *Rubus lasiococcus* | 6.2±5.1 | 2.2±1.4 | 2.2±2.4 |
| | (6) | (8) | (10) |
| *Arnica latifolia* | 0.8±0.4 | 1.2±0.7 | 0.9±0.6 |
| | (13) | (8) | (9) |
| *Tiarella trifoliata* | 1.5±0.5 | 1.0±0.4 | 0.8±0.5 |
| | (15) | (8) | (10) |
| *Valeriana sitchensis* | 2.5±1.2 | 1.1±0.6 | 2.2±1.5 |
| | (10) | (8) | (10) |
| *Erythronium montanum* | 0.7±0.4 | 0.8±0.4 | 0.4±0.2 |
| | (14) | (10) | (10) |

*Mean ± 1 standard deviation. Sample size is given in parentheses.

Different individuals of the same species colonized the tephra at very different rates. The proportion of plant dry weight below, in, and above the tephra was very different among individuals of a species, as indicated by the ranges in Table 2. For the control plants, the percentage of total dry weight above ground varied greatly within all species and reached an eightfold difference in *Tiarella trifoliata* (Table 2).

Even though there was great individual variation, species differences are apparent in the percentage of total dry weight in the tephra (Table 2). *Achlys triphylla*, *Clintonia uniflora*, and *Smilacina stellata*, with long rhizomes and extensive interconnected rhizome systems, had 5–9% of their total dry weight in the tephra in 1981; this increased to 18–23% by 1982. Concomitantly there was a decrease in the percentage of dry weight below the tephra. *Rubus lasiococcus* had only 9% of its total dry weight in the tephra by 1982, but when above-tephra dry weight (including stolons) was included, overall upward movement was comparable to that of species with long rhizomes. *Arnica latifolia* had more than one-third of its total dry weight in the tephra by 1982, probably because of rapid death of the older rhizomes in the old soil. However, its actual weight in the tephra was less than for the other species with long rhizomes (0.42 vs. 0.71 g). Of the two species with short rhizomes, *T. trifoliata* had a much lower dry weight percentage in the tephra than *V. sitchensis* (Table 2). *Erythronium montanum* produced only a little stem or petiole tissue in the tephra annually. In 1982 most species had a lower percentage of dry weight in soil below the tephra than in soil at control sites (Table 2).

### *Distribution of weight among plant parts*

The distribution of dry weight among leaves, stems, and roots varied between years and among species (Fig. 1). The species with large interconnected rhizome or stolon systems (*A. triphylla*, *C. uniflora*, *S. stellata*, and *R. lasiococcus*) all had lower percentages of leaf dry weight and higher percentages of rhizome or stolon dry weight in 1981 than the controls. By 1982 the percentages for tephra plants were all closer to the

TABLE 2. Mean percentage of total plant dry weight above the tephra, in the tephra, and below the tephra for the tephra-buried plants by year of excavation; and above ground and underground for the control plants

| | *Achlys triphylla* | *Clintonia uniflora* | *Smilacina stellata* | *Rubus lasiococcus* | *Arnica latifolia* | *Tiarella trifoliata* | *Valeriana sitchensis* | *Erythronium montanum* |
|---|---|---|---|---|---|---|---|---|
| Above tephra | | | | | | | | |
| 1981 | 10*d*<br>(4–19) | 13*cd*<br>(8–19) | 13*cd*<br>(4–19) | 20*bc*<br>(6–39) | 24*ab*<br>(11–47) | 27*ab*<br>(17–40) | 24*ab*<br>(19–33) | 29*a*<br>(12–44) |
| 1982 | 15*d*<br>(4–32) | 18*bcd*<br>(6–25) | 16*cd*<br>(10–24) | 35*a*<br>(9–62) | 27*ab*<br>(17–44) | 25*abcd*<br>(10–40) | 24*abcd*<br>(14–35) | 26*abc*<br>(15–40) |
| Control, above ground | 18*b*<br>(13–23) | 25*ab*<br>(13–37) | 16*b*<br>(8–22) | 32*a*<br>(17–43) | 36*a*<br>(14–66) | 32*a*<br>(7–58) | 30*a*<br>(17–40) | 29*a*<br>(15–50) |
| In tephra | | | | | | | | |
| 1981 | 9*cd*<br>(1–21)<br>** | 8*cd*<br>(4–15)<br>** | 5*d*<br>(3–9)<br>** | 5*d*<br>(1–8) | 29*b*<br>(19–56) | 12*c*<br>(6–19)<br>** | 40*a*<br>(30–57) | 5*d*<br>(3–7) |
| 1982 | 19*c*<br>(13–31) | 23*c*<br>(7–34) | 18*c*<br>(8–31) | 9*d*<br>(2–19) | 39*b*<br>(23–66) | 19*c*<br>(11–26) | 50*a*<br>(26–62) | 5*d*<br>(2–11) |
| Below tephra | | | | | | | | |
| 1981 | 81*a*<br>(61–96)<br>* | 79*a*<br>(72–88)<br>* | 82*a*<br>(74–92)<br>** | 75*ab*<br>(55–90) | 47*d*<br>(18–67) | 62*c*<br>(49–77) | 36*e*<br>(22–46) | 67*bc*<br>(49–83) |
| 1982 | 66*a*<br>(43–83)<br>* | 60*a*<br>(48–87)<br>* | 67*a*<br>(46–81)<br>** | 56*a*<br>(25–89) | 35*b*<br>(14–61)<br>** | 57*a*<br>(35–75) | 27*b*<br>(12–61)<br>** | 69*a*<br>(55–81) |
| Control, underground | 82*a*<br>(78–87) | 75*ab*<br>(63–87) | 84*a*<br>(78–92) | 68*b*<br>(57–83) | 64*b*<br>(35–87) | 68*b*<br>(42–93) | 70*b*<br>(60–83) | 71*b*<br>(50–86) |

NOTE: The range in individual plant percentages is indicated in parentheses below the mean. Numbers followed by the same letter within a row are not significantly different ($p < 0.05$; Duncan's multiple range test). The significance of differences between 1981 and 1982 and between 1982 and control are indicated by *, $p < 0.05$ or **, $p < 0.01$ between the values for a species ($t$-test). The sample sizes are indicated in Table 1.

control values; values for *S. stellata* were almost identical. The percentage of leaves in the other four species was similar to that in the controls except for *V. sitchensis*, which had a lower percentage in both 1981 and 1982 (Fig. 1).

For both *T. trifoliata* and *V. sitchensis* the percentage of dry weight contributed by rhizomes in 1982 was well above control levels, while the percentage attributable to roots was much below control values; the proportions of rhizomes and roots were closer to the controls in 1981 (Fig. 1). For both species actual dry weight of rhizomes decreased (to 87 and 53%; 1982 values expressed as percentage of 1981 values) while root weight dropped (to 49 and 31%) from 1981 to 1982. The changes in proportions apparently resulted from a die-off of roots. *Erythronium montanum* plants had only a few small roots (Fig. 1). The percentage of roots on the species with long rhizomes or stolons was roughly equivalent to control values in both years. *Achlys triphylla*, *S. stellata*, and *A. latifolia* had a lower percentage of roots than the other species except *E. montanum*. *Arnica latifolia* had few roots while *A. triphylla* and *S. stellata* had numerous fine roots and thick rhizomes so that percent root weight was relatively low.

### *Movement into tephra*

Species can be grouped by the pattern of movement of their roots and rhizomes, stolons, or corms into the tephra. *Achlys triphylla*, *C. uniflora*, and *S. stellata* responded similarly; the percent root and rhizome in the tephra, small in 1981, had increased greatly by 1982 (Fig. 1). Rhizomes in the tephra were not, in general, notably different from rhizomes in the old soil. The proportion of roots in the tephra was similar to the proportion of rhizomes for *S. stellata*, but lower for *A. triphylla* and *C. uniflora*. *Smilacina stellata* produces roots on its current-year rhizome but the other two species often do not.

The percentage of stolon dry weight in and above the tephra for *Rubus lasiococcus* was similar to that in tephra for rhizomes of *A. triphylla*, *C. uniflora*, and *S. stellata* (Fig. 1). Percentage of root weight in the tephra was lower for *R. lasiococcus* than for any other species except *E. montanum*. *Rubus lasiococcus* roots grow indefinitely and can reach a very large size (Antos and Zobel 1984). Although *R. lasiococcus* stolons were spreading rapidly over the surface of the tephra and producing numerous small, new roots, most of the root mass was still concentrated in a few large roots in the old soil.

*Arnica latifolia*, with its relatively rapid turnover of long rhizomes, quickly colonized the tephra; over half of both root and rhizome dry weights was in the tephra in 1982 (Fig. 1). *Arnica latifolia* had a higher percentage of its roots in the tephra than any other species in 1982.

For *V. sitchensis* and *T. trifoliata* most of the rhizome in the tephra was produced during initial growth through the tephra; little rhizome growth occurred subsequently (Fig. 1). *Valeriana sitchensis* rhizomes in the tephra were of similar weight per unit length as those in old soil. In contrast, *T. trifoliata* rhizomes in the tephra were thinner and weighed less per unit length. *Valeriana sitchensis* had well-developed roots in the tephra but *T. trifoliata* did not, especially during 1981. *Tiarella trifoliata* roots grow for many years and can attain a large size. *Valeriana sitchensis* roots are of similar size all along the rhizomes.

The corm of *Erythronium montanum* showed little or no sign of upward movement and produced no roots in the tephra (Fig. 1).

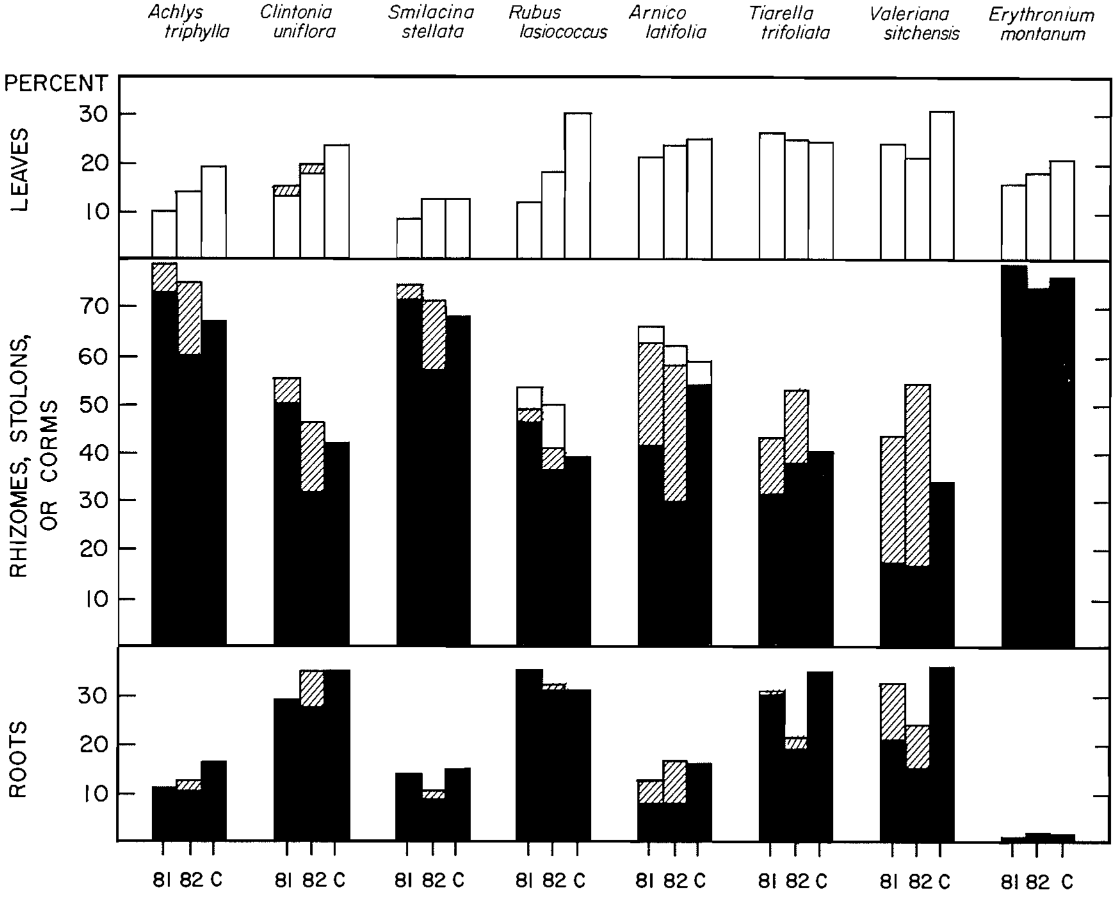

FIG. 1. Percent total plant dry weight contributed by roots; rhizomes, stolons, or corms; and leaves, for plants in the tephra during 1981 (81) and 1982 (82) and for control plants (C). The percentages in old soil (■), tephra (▨), and air (□) are indicated. Determinate aerial stems which support the leaves of *Smilacina stellata* are not included with the leaf dry weight; they represented 4–5% of total plant dry weight. The values for *Erythronium montanum* are for vegetative plants only.

### *Characteristics of emergent shoots*

In addition to responses of whole plants, we can examine the process by which individual stems of buried plants grew into the tephra and succeeded in producing aerial parts. Most species grew through the tephra by producing a shoot only 1–2 cm longer than the tephra was deep, indicating a fairly direct and vertical course to the surface (Table 3). *Arnica latifolia* was the notable exception; the rhizomes often followed tortuous routes and sometimes coiled under an obstacle. *Arnica latifolia* rhizomes were very weak, had little ability to push directly through the tephra crust, and had to reach the surface before leaves could be produced. In contrast, *A. triphylla*, *C. uniflora*, and *S. stellata* produced leaves or determinate aerial shoots from rhizomes well below the tephra surface. Typically, their rhizomes angled up into the tephra and from this the petiole or aerial shoot grew nearly vertically. In 1982 rhizomes were closer to the surface; thus the annual shoots of the three species penetrated 2–5 cm of tephra versus 6–7.5 cm in 1981. *Rubus lasiococcus* stolons and *T. trifoliata* and *V. sitchensis* rhizomes grew vertically and their length in excess of tephra depth was caused by growth around obstacles. Shoots of *Erythronium montanum* grew directly through the deposit even though they were very fragile.

The length in the tephra of rhizomes that developed following each successful penetration through the tephra increased most between years for *C. uniflora* and *S. stellata* (Table 3). The rhizomes of these species moved upward into the tephra and sometimes proliferated. The rhizomes resulting from one entry into the tephra sometimes supported more than one aerial shoot, especially in 1982. The length of *Arnica latifolia* rhizomes increased between years as new rhizomes formed from the one that originally reached the surface. *Rubus lasiococcus* stolons did not increase in length in the tephra; once they reached the surface all further growth occurred on the surface. The length of *Tiarella trifoliata* rhizomes increased substantially between years because of subsurface branching, although *V. sitchensis* rhizome length did not change much.

The number of roots in the tephra per site of emergence increased from 1981 to 1982 for most species. The decrease observed for *V. sitchensis* reflects smaller overall plant size in the 1982 sample.

## Discussion

Seven of the eight species moved their perennating buds into the tephra; these buds reached approximately their normal depth below the surface by the third season following the eruption. *Achlys triphylla*, *Clintonia uniflora*, and *Smilacina stellata* produced leaves from deeply buried rhizomes. In contrast, leaves of *Rubus lasiococcus*, *Arnica latifolia*, *Tiarella trifoliata*, and *Valeriana sitchensis* generally were not produced until the perennating buds were within 1 to 2 cm of the tephra surface. There is no evidence for upward movement of perennating buds of *Erythronium montanum*; shoots of this species must penetrate the tephra annually. Even though *Erythronium*

TABLE 3. Mean and standard deviation (in parentheses) of tephra depth and plant characteristics associated with locations where a buried plant grew into the tephra and succeeded in emerging above the tephra

| | $n$[a] | Tephra depth, cm | Stem length,[b] cm | No. of new rhizomes[c] | Rhizome length,[d] cm | No. of roots |
|---|---|---|---|---|---|---|
| *Achlys triphylla* | | | | | | |
| 1981 | 19 | 10.7 (2.6) | 12.9 (3.5) | 1.3 (0.7) | 13.7 (9.5) | 11.6 (9.2) |
| 1982 | 14 | 12.3 (2.2) | 14.2 (3.6) | 1.1 (0.9) | 19.2 (12.5) | 20.5 (13.8) |
| *Clintonia uniflora* | | | | | | |
| 1981 | 15 | 11.1 (2.0) | 12.2 (3.0) | 1.6 (0.6) | 11.0 (6.0) | 1.7 (1.6) |
| | | | | | ** | ** |
| 1982 | 11 | 12.7 (2.0) | 14.2 (2.7) | 2.1 (0.7) | 22.9 (8.4) | 4.5 (1.8) |
| *Smilacina stellata* | | | | | | |
| 1981 | 19 | 7.6 (2.3) | 7.9 (2.5) | 0.8 (0.6) | 3.3 (4.8) | 10.9 (12.7) |
| | | | | | | ** |
| 1982 | 11 | 7.6 (1.5) | 8.5 (2.4) | 1.3 (0.5) | 12.3 (11.3) | 41.4 (40.1) |
| *Rubus lasiococcus* | | | | | | |
| 1981 | 16 | 13.5 (2.3) | 15.1 (3.0) | 2.3 (0.8) | 17.3 (5.4) | 6.6 (6.3) |
| | | | | ** | | |
| 1982 | 8 | 14.3 (1.9) | 16.5 (3.1) | 4.1 (1.6) | 17.8 (6.4) | 10.3 (7.1) |
| *Arnica latifolia* | | | | | | |
| 1981 | 13 | 14.3 (1.9) | 21.1 (5.4) | 0.5 (1.1) | 23.2 (5.8) | 8.5 (3.9) |
| | | | | | ** | |
| 1982 | 11 | 14.7 (1.7) | 21.6 (4.8) | 1.3 (1.4) | 32.7 (7.1) | 13.2 (8.0) |
| *Tiarella trifoliata* | | | | | | |
| 1981 | 16 | 12.1 (2.3) | 13.3 (3.1) | 0.1 (0.3) | 13.6 (3.6) | 7.4 (3.8) |
| | | * | * | ** | ** | ** |
| 1982 | 8 | 14.5 (2.5) | 17.5 (5.3) | 0.8 (0.7) | 23.8 (11.7) | 13.3 (4.2) |
| *Valeriana sitchensis* | | | | | | |
| 1981 | 10 | 14.4 (1.5) | 16.4 (1.9) | 0.1 (0.3) | 16.6 (2.0) | 20.7 (10.8) |
| | | | | | | ** |
| 1982 | 9 | 14.8 (2.2) | 17.7 (2.7) | 0.0 (0.0) | 17.7 (2.7) | 8.6 (4.1) |
| *Erythronium montanum* | | | | | | |
| 1981 | 15 | 13.0 (2.4) | 14.0 (3.2) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |
| 1982 | 10 | 13.7 (2.7) | 15.0 (3.8) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |

[a] Number of locations examined.

[b] Shortest length of plant stem (and sometimes petiole) between entrance into and exit from the tephra.

[c] Number of new, rapidly growing rhizome or stolon tips.

[d] Total length of rhizome or stolon in the tephra.

NOTE: Significant differences between 1981 and 1982 are indicated as follows: *, $p < 0.05$; **, $p < 0.01$ (Mann–Whitney $U$-test).

initially survived burial about as well as other species (Antos 1984), this resource drain could result in increased mortality rates.

The species with extensive rhizome systems, *A. triphylla*, *C. uniflora*, and *S. stellata*, responded similarly to burial by tephra. Rhizomes angled upward into the tephra, and produced aerial shoots from depths as great as the tephra base. Usually only one, sometimes two, shoots emerged on plants that normally would have had several. Thus, the ratio of leaf weight to weight of underground tissue decreased. Much of this imbalance had been corrected by 1982 because of rhizome mortality and increase in the number of aerial shoots.

Buried stolons of *R. lasiococcus* grew straight up through the tephra and then spread rapidly across the tephra surface. Rhizome tips of *A. latifolia* turned upward and emerged to yield aerial shoots. *Arnica latifolia* had a higher percentage of its rhizomes in the tephra than the other species with long rhizomes, primarily because of its more rapid rhizome turnover.

The two species with short rhizomes, *Tiarella trifoliata* and *Valeriana sitchensis*, responded similarly in a qualitative sense. The rhizome tip turned upward and elongated rapidly until reaching the surface, a pattern characteristic of most species with short rhizomes in the area (Antos and Zobel 1985*b*). This morphological transformation allowed the plants to survive, but required a much greater than normal resource allocation to rhizome growth.

There are virtually no data on the amount of plant biomass present in deposits that have buried plants. For a sand dune grass, Maun and Lapierre (1984) reported ratios of biomass in the burying deposit to that in the original substrate which are higher than for any of the species we studied. The rate at which a plant moves its rhizomes and roots into a burying deposit is a function of normal rates of rhizome and root turnover. The species that we studied that have large, old rhizome or stolon systems had the lowest percentages of biomass in the tephra, except for the species that did not relocate perennating buds upward. Species with perennating structures that are not relocated upward, or with extensive, old rhizome systems are slowest at moving their biomass into a covering material.

Except for *Erythronium montanum*, individuals representing all of the species have in large part reestablished their normal growth form relative to the new surface; even so, their long-term survival in the tephra is not yet assured. As of 1982, all species retained considerable live root tissue in the old soil. Survival will ultimately depend on the ability of plants to utilize the tephra or send roots into the buried soil. It appears that most nutrient concentrations in tephra under a forest canopy are similar to those in the buried soil (Antos 1984); thus, the tephra may be a relatively good growth medium for plants.

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